

Physiological Progenesis in Cephalopod Molluscs

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The coleoid cephalopods (cuttlefish, squid and octopus) arose from their shelled ancestors during the late Devonian; they diversified in the Jurassic but did not radiate substantially until the Tertiary. Since then they have coevolved with the fish (1). Squid are less efficient energetically than fish (2) but have survived alongside them by evolving highly opportunistic reproductive and feeding strategies (3, 4) as well as rapid jetting and inking for escape and defense. Little is known about the life history strategies of the fossil forms, but the only surviving shelled cephalopods, the nautilus, have relatively long life spans and are iteroparous; that is, in common with most members of other molluscan classes, they breed more than once during their lives. In contrast, all other living cephalopods are generally short lived (usually 1 year) and have monocyclic reproduction and a semelparous life history. The short-lived semelparous coleoids are typified by the mid-latitude ommastrephid squid which provide the basic model considered here. This family is relatively primitive and biologically well known. Its members are essentially monocyclic, but some species may spawn their eggs in batches (5, 6), although there is no evidence of this in laboratory spawnings (7). Most loliginid squid, at least in temperate seas, have a life cycle similar to that of the ommastrephids, despite having different spawning habits. A comparison of the lifetime energetics and growth pattern of benthic, iteroparous molluscs with those of the pelagic, semelparous ommastrephids shows that, although some squid may attain a length of 1 m or more, the allocation of their energy resource among growth components is essentially characteristic of the early life, especially the first year, of iteroparous forms. The lifetime energy budget of these squid thus seems to have evolved by physiological progenesis, a process in which

maturation is accelerated while other aspects of the physiology are more typical of the juvenile.

The life cycle of most benthic marine molluscs (bivalves and gastropods) is characterized by a relatively short egg and larval stage, a long adult life span (usually several years), and iteroparity (8). Feeding rates of herbivorous and carnivorous species decline relative to body mass over the lifetime, and the mass exponent for feeding rate is invariably less than for metabolic rate (9). These allometric relationships between consumption rate, metabolic rate, and body mass mean that, as body size increases, the amount of energy produced by food consumption decreases relative to the amount of energy lost as heat. The relative scope for growth therefore decreases with size, and this is the physiological basis for the steadily decreasing gross and net growth efficiency with age (10). Annual production of somatic tissue reaches a maximum during the first half of the life span and declines thereafter, whereas gamete production increases asymptotically. Somatic production exceeds gamete production during early life, but is later exceeded by gamete production, which eventually dominates tissue growth. Lifetime energy budgets have been estimated for some bivalves and gastropods (11, 12), and the general pattern of energy allocation is illustrated in Figure 1a. Lifetime energetics is dominated by respiratory losses in the form of heat. A substantial proportion of total production is allocated to shell organics, and this, together with the energy cost of mineralization (13), reduces the energy available for tissue growth in these benthic forms.

The physiological energetics of *Nautilus*, which probably resembles that of the ancestors of the living coleoids in many respects, differs substantially from that of the coleoids with respect to reproduction (14). *Nautilus* has a life span of more than 4 years, and its reproduction is iteroparous, so in many respects its lifetime energy budget resembles that of the iteroparous benthic molluscs.

Relative to most iteroparous molluscs, including *Nautilus*, the life cycle of the semelparous cephalopods is char-

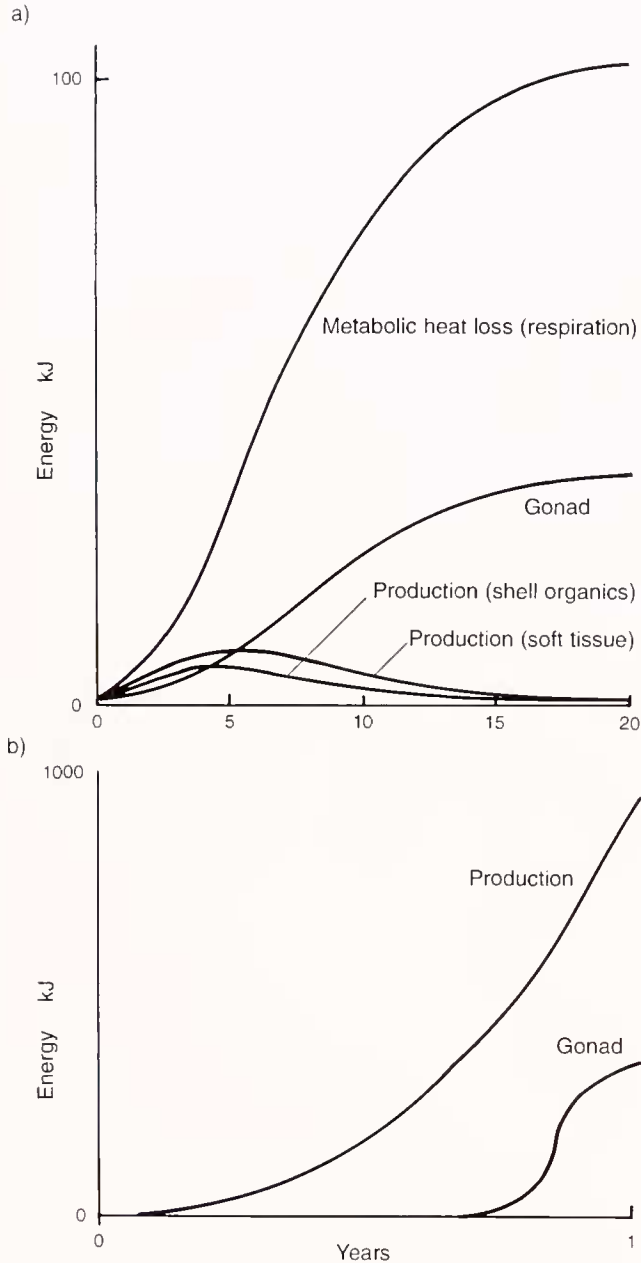


Figure 1. Energy, in kilojoules (kJ), allocated to the different components of growth and metabolism: (a) over the 20-year lifetime of a long-lived, iteroparous benthic bivalve (*Ostrea edulis*); (b) over the one-year lifetime of a short-lived semelparous cephalopod (*Illex argentinus*).

acterized by long egg, paralarval, and juvenile phases, and by a short adult life. Feeding and metabolic rates are higher than in other molluscs (15), and empirically determined mass exponents for feeding and metabolic rate are higher than in benthic molluscs—0.79 [feeding] and 0.96 [metabolism] for the squid *Illex illecebrosus* (16) compared with mean values of 0.58 ± 0.12 [feeding] and 0.70 ± 0.13 [metabolism] for 36 and 50 benthic species,

respectively (9). The mass exponent for metabolic rate has long been thought to be close to 1.0 in small organisms (< 50 mg) and approaching 0.75 in larger ones (17). This exponent has been suggested to derive from the weighted sum of body surface area and volume (18). Squid appear to fall between the predicted values for large and small organisms. The exponent for feeding rate is lower than for metabolic rate, but the difference between these exponents in the *I. illecebrosus* example is less than in the longer-lived iteroparous molluscs (9), implying relatively higher scope for growth at larger body size in the squid. This is reflected in relatively high growth efficiencies (15). Somatic tissues grow for most of the squid life span, but gonad growth is rapid once sexual maturation is initiated. *Illex argentinus*, with a life span of about a year, starts to mature in about 7 or 8 months and reaches full maturity by 12 months (19). Lifetime production of soma and gonad in *I. argentinus* has been estimated from data on growth and allometry combined with biochemical composition (19, 20). The pattern of energy allocation among soma and gonad in the squid differs fundamentally from the pattern in the long-lived iteroparous molluscs (Fig. 1b). Production of somatic tissue continues until full sexual maturity; and even in the latter part of the life span, when the squid is reaching maturity, somatic growth remains in excess of gonad production. This pattern of energy allocation among soma and gonad closely resembles that of the first year of the longer-lived iteroparous molluscs. Suitable data on lifetime metabolic heat losses in cephalopods are not available for comparison with the benthic forms.

The declining relative scope for growth and increasing allocation of energy to reproduction is the mechanism underlying the form of the asymptotic growth curve followed by these longer-lived iteroparous molluscs. The von Bertalanffy growth function is commonly used in ecology and fisheries science to model asymptotic growth of animals (21) and has provided an adequate fit to most data for annual growth increments in iteroparous molluscs. The equation is generally given as:

$$l_t = L_\infty [1 - e^{-K(t - t_0)}]$$

in which l_t is length at time t , L_∞ is length at infinite age, K is the rate constant at which L_∞ is approached, and t_0 is effectively a scaling factor that displaces the curve along the age axis to fit the data. Seasonality of growth has also been modeled by substituting day-degrees for time in the von Bertalanffy model (22, 23):

$$l_D = L_\infty [1 - e^{-K_D(D - D_0)}]$$

in which l_D is length at D day-degrees, K_D is the rate constant determined as K/D_y (D_y is the annual sum of day-degrees) and $D_0 = t_0 \cdot D_y$. This models the effects of

seasonal temperature variation only and not, for example, changes in food available to suspension feeders grazing on seasonal phytoplankton blooms. The von Bertalanffy model rarely, if ever, fits growth during the juvenile phase (usually the first year of life), hence the necessity for the mathematical convenience of the term t_0 , as the fitted model rarely passes through the origin. The poor fit of the von Bertalanffy function to growth of the juvenile phase is probably due to the combined effects of seasonality of growth in the first year and different patterns of energy allocation during the pre-reproductive phase of early development.

The high growth efficiency of squid, together with their relatively low investment in gonadal growth, results in high growth rates throughout the life span (24). This efficiency is accentuated by their semelparity, because the reduction in growth rate, due in iteroparous forms to the energetic costs of repeat spawning, is not experienced. The age of ommastrephids taken from the field has been estimated from daily growth increments in the statolith. These data show that growth in mantle length of adults up to sexual maturity can generally be fitted by a simple linear model (19, 25). But there are no data covering the whole life span of ommastrephids, including the brief post-spawning phase, so the form of the growth curve towards the end of life is not known. The allometric coefficient in ommastrephids is generally close to 3.0 (24), so the linear phase of growth in mantle length is accompanied by a power curve reflecting growth in mass. Where detailed measurements have been made on squid, growth in mass is best fitted by an exponential growth function for early life and a power function for the latter phase (24, 26). Modeling studies also suggest that lifetime growth is influenced by temperature, especially in the post-hatching period (27, 28). This is reflected in field data, which indicate different growth patterns in squid hatched in different seasons and, by inference, at different temperatures (19, 29, 30), as well as in laboratory studies (27) in which squid were exposed to different water temperatures after hatching.

Squid appear to exhibit physiological progenesis in the sense that they reach full maturity over a short life span during which their lifetime energy budget resembles that typical of the early life of iteroparous molluscs, a time when growth rate and growth efficiency are relatively high, when production is dominated by somatic growth, and when reproductive investment (proportion of body mass released as gametes) is relatively low. In squid, low reproductive investment is compensated for by traits that minimize juvenile mortality: relatively large hatchlings, direct development, protective egg coatings, and the rapid, jet-propelled escape response possessed even by hatchling squid (3). Although the evolutionary processes of progenesis and neoteny have usually been attributed

to morphological phenomena (paedomorphosis) (31), applying the concept of progenesis to physiological energetics provides a useful insight into the evolution of patterns of cephalopod growth and reproduction.

For much of their life span, squid occupy the juvenile phase of the generalized molluscan life cycle that is not readily fitted by the von Bertalanffy growth function. Because this function rarely fits the growth data for squid or other cephalopods (32), they have been compared with larvae of other taxa that do not grow asymptotically (33). If, as has been argued, the von Bertalanffy function is fundamentally applicable to squid (34), they probably die before, or very soon after, approaching the asymptotic phase. The principal factors that underlie the complicated and highly variable growth trajectories of these molluscs are changes in the allocation of energy resources between soma and gonad; seasonality of growth rate, modulated by food availability and temperature; and the confounding effects of hatching season on lifetime growth rate. The underlying lifetime pattern of energy allocation and the consequent growth characteristics of the cephalopods suggest that these traits have evolved through physiological progenesis, in which sexual maturation has been accelerated, while the energy budget retains features found in the juvenile phase of other classes of molluscs.

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